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Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitary than communally

Davina L. Hill[1*], Neville Pillay[1] and Carsten Schradin[1,2,3]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

[2]Université de Strasbourg, IPHC-DEPE, 23 rue Becquerel 67087 Strasbourg, France

[3]CNRS, UMR7178, 67087 Strasbourg, France

[*]Correspondence author and present address: Animal and Veterinary Sciences, Scotland's Rural College (SRUC), King's Buildings, West Mains Road, Edinburgh EH9 3JG, UK. (davina.hill@sruc.ac.uk)

Key-words alternative phenotypes; breeding synchrony; cooperative breeding; phenotypic plasticity; plural breeding; polyphenism; reproductive competition; single breeder; social flexibility; sociality

Summary

1. Alternative reproductive tactics (ARTs) are discrete reproductive phenotypes governed by decision-rules called strategies. ARTs are fixed for life in species with alternative strategies, while tactic expression is plastic in species with a single strategy. ARTs have been investigated in males of many species, but few studies have tested whether the same theoretical framework applies in females.
2. Female striped mice (*Rhabdomys pumilio*) employ three ARTs: communal breeders give birth in a nest shared with female kin and a breeding male, and show allo-parental care; returners give birth away from the shared nest and later return to it; and solitary breeders give birth away from the shared nest and do not return to the group.
3. Here, studying free-living female striped mice over six breeding seasons, we tested whether ARTs arise from alternative strategies or a single strategy.
4. We also asked to what extent stochastic extrinsic factors explain whether individuals become solitary rather than group-living.
5. Females switched tactics, consistent with a single strategy, so we tested whether this represented a mixed or conditional single strategy. Only the latter predicts differences between ARTs in traits indicating competitive ability, such as body mass or age, before individuals adopt a tactic. We weighed females at conception when they were still group-living to eliminate potential confounding effects of gestation and subsequent social tactic (solitary- versus group-living) on body mass.
6. Females that went on to use a solitary ART were heavier than those that became communal breeders and returners, in support of a conditional strategy.
7. Importantly, solitary breeders also arose through extrinsic factors (mortality of all adult female group members). They weighed less than females that became solitary

26 while relatives were alive, but did not differ in body mass from communal breeders
27 and returners.
28 8. We conclude that ART theory applies to both sexes, with female striped mice
29 following a conditional single strategy. Future studies should consider the possibility
30 that phenotypes that superficially resemble evolved tactics might also arise through
31 non-adaptive extrinsic causes.
32

Introduction

A primary aim of life history theory is to understand the factors that influence reproductive decisions. *Alternative reproductive tactics* (ARTs) are discrete reproductive phenotypes shown by different members of the same sex and population and governed by genetically-based decision-rules called *strategies* (Dominey 1984; Gross 1996). Individuals following alternative tactics differ in behavioural, morphological, physiological and/or life history characteristics. Individuals are said to use *alternative strategies* when different tactics are controlled by different genotypes (Gross 1996), and *single strategies* when a single genotype controls different tactics (Schradin & Lindholm 2011). At the phenotypic level, ARTs are fixed for life in individuals following alternative strategies, while their expression is plastic under a single strategy (Fig. 1).

The term single strategy was introduced to describe systems where one decision-rule can produce multiple phenotypes (Fig. 1) regardless of whether fitness differences between ARTs occur (which can depend on environmental conditions) (Schradin & Lindholm 2011). Such decision-rules are traditionally divided into mixed and conditional strategies (Fig. 1). A *mixed strategy* occurs when tactics are expressed on a probabilistic basis rather than in response to environmental or individual-level cues (Dominey 1984). Individuals employing a *conditional strategy*, by contrast, are predicted to select the tactic that generates the highest fitness returns for their prevailing state or status (status-dependent selection model; Gross 1996). Individuals frequently differ in continuous traits associated with competitive ability, such as body mass or age. When the tactic that yields the highest fitness (often called the bourgeois tactic) is also the most costly to employ, only the most competitive individuals will be able to use it (Gross 1996). Less competitive individuals will thus employ a different tactic that yields a lower

fitness but is the highest fitness they can achieve at the time, known as 'making the best of a bad job' (Dawkins 1980). Under a conditional strategy, individuals should express a particular tactic when they pass a threshold (*switchpoint*) for the indicator trait after which the fitness benefits for that tactic are greater than what they could achieve using an alternative tactic (Hazel, Smock & Johnson 1990). They may switch from one tactic to another, for example, when they reach a certain age or size. The environmental-threshold model predicts that selection acts upon heritable genetic variation for the position of the switchpoint, so different individuals might express a given tactic at different values of the indicator trait (reviewed in Tomkins & Hazel 2007).

ARTs have been studied extensively in males, but are less well understood in females. Female ARTs include monandry versus polyandry in horseshoe crabs (*Limulus polyphemus*) (Johnson & Brockmann 2012) and brood parasitism versus maternal care in goldeneye ducks (*Bucephala clangula*) (Åhlund & Andersson 2001). ARTs often evolve where there is pronounced intra-sexual variance in fitness and intense reproductive competition (Shuster 2008). These conditions apply more frequently in males than in females, which probably explains the greater prevalence of male ARTs (Neff & Svensson 2013). However, intense reproductive competition also exists between females (Clutton-Brock 2009), and the number of studies of female ARTs has increased in recent years, suggesting that they were previously overlooked. This balance needs to be redressed to achieve a comprehensive, sex-independent understanding of ARTs.

Few studies to date have investigated the factors leading to the evolution of female ARTs and whether the theory governing male ARTs applies to females. The striped mouse (*Rhabdomys pumilio*) is a good species in which to address these issues because ARTs occur in both sexes,

with males and females either breeding solitarily or in groups. Breeding groups typically consist of 2-4 closely related females, one male and their communal offspring (Schradin & Pillay 2004). Communally-breeding females often give birth synchronously and provide allo-parental care, including allo-nursing (Schradin, Kinahan & Pillay 2009a; Schubert, Pillay & Schradin 2009). Nevertheless, reproductive competition occurs between females through aggression and infanticide (Schradin, König & Pillay 2010), and females can become solitary during the breeding season if unoccupied territories are available (Schradin, König & Pillay 2010; Schoepf & Schradin 2012a). While the ratio of communal to solitary females increases with increasing population density, both solitary and group-living females co-occur under most conditions (Schradin, König & Pillay 2010; Schoepf & Schradin 2012a). In addition to these solitary and communal breeding female tactics, we report here for the first time the tactic of *returner*, where females give birth away from the natal group but later return to it.

Group-living females might become solitary as part of a strategy to optimize fitness or alternatively because of extrinsic factors that constrain them to rear young alone (Schradin 2013). Groups are limited to close kin in many social species, and these groups can be reduced to a single solitary individual by natural mortality. This can occur in populations with small group sizes and high predation, such as Callitrichid primates (Anzenberger & Falk 2012). In the absence of information on group history, such individuals might be mistakenly assumed to be following a solitary ART. However, in such cases, solitary-living is not the result of a strategy (an evolved set of rules), and cannot be explained by ultimate or proximate causes at the individual level (Schradin 2013). Therefore, when observing solitary versus group-living members of the same population, it is important to consider the possibility that solitary-living is not a tactic, but the result of stochastic processes. To our knowledge, this has not been considered in any previous study on ARTs.

Here, we explored the following questions in female striped mice: (i) Do ARTs arise from alternative strategies or a single strategy? We addressed this by testing whether females switched ARTs, which would indicate a single strategy. Females did switch ARTs, and so we asked (ii) whether this represented a mixed or a conditional strategy. Under a conditional (but not mixed) strategy, females that go on to adopt different tactics are predicted to differ from each other in individual-level traits that reflect competitive ability. We examined body mass because it is associated with competitive ability (Schradin 2004) and aggression (Schoepf & Schradin 2012b) in this species, and because male striped mice following alternative tactics differ in body mass (Schradin *et al.* 2009b). To decouple the predicted effect of body mass on tactic choice from the confounding effects of following different tactics on body mass, all females were weighed when they were still group-living. We also considered age, which is related to aggression in striped mice (Schoepf & Schradin 2012b) and to rank in many co-operatively breeding species (Creel *et al.* 1992). We predicted that females that go on to breed solitarily would be heavier and/or older than communal breeders. Next, we examined breeding synchrony to test whether females leave the group to avoid reproductive competition. In communally-breeding groups, earlier-born litters suffer an increased risk of infanticide from gestating females, while later-born litters may be unable to compete with older ones (Hodge, Bell & Cant 2011). We predicted that group-living females would be more closely synchronized with nestmates than with females from other groups, and that females that were less synchronized with nestmates would be more likely to adopt a solitary or returner tactic than to breed communally. Finally, we asked (iii) whether solitary breeding is always the outcome of a strategy or if it can also arise from entirely extrinsic factors (mortality of all other adult female group members). If the latter scenario occurs, we would expect females constrained to breed solitarily by the death of relatives to be of a lower body

mass or age than solitary breeders with living relatives (which are predicted under ii to be subject to status-dependent selection for increased body mass or age), but to be similar in body mass and age to communal breeders.

Materials and Methods

STUDY SITE

Fieldwork took place every month during the years 2005 to 2010 in Goegap Nature Reserve, Northern Cape Province, South Africa (S 29 41.56, E 18 1.60). The study area is Succulent Karoo and consists of an open habitat of shrubs, grass and sandy areas. It receives 180mm precipitation *per annum*, which mostly falls between April and July. Minimum ambient temperature (T_a) was recorded in the shade 5cm above the ground at the study site each day.

LIVE-TRAPPING AND BEHAVIOURAL OBSERVATIONS

Striped mice are diurnal and nest in shrubs at night. They rarely experience more than one breeding season, so each year of study represents a new generation. Individuals were captured using Sherman-type live-traps (26×9×9cm) baited with bran flakes, sunflower oil and salt. Traps were set in the shade close to nest sites at dawn and in the afternoon, and checked twice in the morning and once at dusk, 30-45 minutes after being set. We placed 3-20 traps (depending on group size) at several nest sites for 3-4 consecutive days throughout the year to allow each group to be monitored on rotation every two weeks. Newly-trapped individuals were provided with numbered aluminium ear-tags (National Band and Tag, Newport, KY) for identification, and marked with hair dye (Inecto, Pinetown, South Africa) so that they could be recognized during behavioural observations at nest sites (see below).

158 Adults were fitted with MD-2C radio-collars (Holohil, Canada), which weighed 2.5g,
159 representing 5.4±0.07% of the body mass of non-gestating females (n=181 records from 110
160 females). Females were weighed to the nearest gram using an electronic balance, and nipples
161 were classified as pink and elongated (suggestive of lactation), otherwise visible or not
162 visible.
163
164 Juveniles (body mass <30g) were assumed to originate from the nest where they were first
165 trapped and observed affiliating with group members during behavioural observations. This
166 method was validated using microsatellite markers (Schradin & Lindholm 2011).
167 Behavioural observations took place at nest sites at dusk when striped mice were returning
168 from the day's foraging. We observed marked individuals through binoculars for 30 minutes
169 from a distance of ~10m, and recorded affiliative and aggressive interactions as described in
170 Schradin and Pillay (2003). Observations were carried out on all focal groups on rotation
171 throughout the year, except that a given group was not subject to both trapping and
172 behavioural observations on the same day. As genetic data show that female group members
173 are close kin (C. Schradin and A. K. Lindholm, unpublished data), we refer to females that
174 nested together (or did so before becoming solitary) as 'relatives'.
175
176 RADIO-TRACKING
177 Striped mice were radio-tracked 4-5 nights a week throughout the breeding season using an
178 AR8000 wide-range receiver (AOR, Tokyo, Japan) and an H-antenna. We approached
179 potential nest sites from different angles until we located the source of the radio-signal. We
180 assumed that individuals were sharing a nest when their signals derived from the same
181 position. This allowed us to determine the location of nests, the identity of all adults in a nest
182 and the date that individuals changed nest sites. Individuals leave the nest by day to forage, so

we also radio-tracked them once during the day to confirm that radio-collars had not been discarded in the nest. Locations of individuals and nests were recorded using an eTrex Venture GPS (GARMIN, Olathe, KS), which was accurate to ~5m at our study site. We maintained continuity of group identities between breeding seasons by radio-tracking one female from each group during the non-breeding seasons, when group membership is stable (Schoepf & Schradin 2012; Schradin, König & Pillay 2010). Radio-collars were removed from all other group members at the end of each breeding season.

DETERMINATION OF ALTERNATIVE REPRODUCTIVE TACTIC

Striped mice give birth in the austral spring (August to December). For each female fitted with a radio-collar, we plotted body mass records from July to January of each year against the date. We examined individual plots for the rise and sudden fall in body mass indicative of gestation and parturition. We assumed that parturition occurred on the median day within each trapping interval (the period between a female's last trapping antepartum and her first trapping postpartum) unless we could refine our estimate from observational data. We checked whether the estimated parturition date was consistent with a change in lactation status. Females were classified as *nesting communally* (sharing a nest with ≥1 adult female) or *not nesting communally* on the night before parturition. The latter category was divided into three subcategories: a) *returners*: those that nested with their original group ≥1 night after parturition; b) *solitary breeders with relatives*: those that did not nest with the group after parturition although former (female) nestmates were still alive; and c) *solitary breeders without relatives*: females whose female nestmates were no longer living. We refer to the four categories (communal breeder, returner, solitary breeder with relatives, solitary breeder without relatives) as *reproductive phenotypes*, and the first three of these categories (i.e. those that are not determined by mortality of all female relatives; see Introduction) as *ARTs*. We

ensured that solitary females were not nesting with unmonitored females by only considering groups where all adult females were wearing radio-collars when relatives gave birth, and by observing the identity of individuals returning to nests during behavioural observations.

ESTIMATION OF AGE AT PARTURITION AND BODY MASS AT CONCEPTION

Age at parturition (AP) was calculated as the difference between a female's estimated parturition date and her date of birth; date of birth was estimated from the population-specific growth curve in Schradin, Schneider & Yuen (2009c). We estimated the date that females conceived by subtracting 23 days (the minimum period between litters in captive striped mice (Brooks 1982)) from the estimated parturition date. To estimate *body mass of females at conception* (BMC) we used the closest morning body mass record available up to 10 days before or three days after the estimated conception date. We only used morning data because females weighed less in the morning than at dusk (morning: 39.4±2.37g, n=12,515 observations from 1917 females; dusk: 42.6±2.37g, n=6398 observations from 1602 females; β=3.17±0.13, t=23.84, P<0.001, controlling for individual identity and year). BMC records were considered 'missing' if no morning values were available or if females were known to be gestating. Missing values for BMC and AP were filled in using multiple imputation (Appendix S1).

STATISTICAL ANALYSIS

We retained for statistical analysis all parturitions occurring between 1st August and 31st December in 2005 to 2010 where parturition date and reproductive phenotype could be determined (n=243 parturitions from 132 females from 33 groups; Table 1). Four females gave birth in two consecutive breeding seasons (two in 2005-06 and two in 2007-08); the remaining 128 individuals bred in a single season. Variation in monitoring effort is likely to

233 be a common feature of longitudinal field studies like ours, but is rarely reported. We present
234 annual survey effort in Table 1. *Parturition trapping interval* (PTI) and *radio-tracking effort*
235 were not associated with reproductive phenotype (Generalized and General Linear Mixed
236 effects Models, respectively, controlling for individual identity, group identity and year: PTI
237 $P \geq 0.059$; radio-tracking effort $P \geq 0.128$, adjusted for multiple comparisons). Mean annual
238 breeding synchrony was not correlated with PTI ($r_s=0.49$, $P= 0.356$, $n=6$).
239

240 **Table 1.** The numbers of groups and 'focal' females (i.e. females that gave birth while they and all
241 female relatives were fitted with radio-collars), the number of parturitions for which radio-tracking
242 data were available, adult population density at the start of the breeding season (Sept), the mean
243 trapping interval within which females gave birth, and mean radio-tracking effort (the number of
244 nights a female was tracked as a percentage of the number of nights she wore a radio-collar). Each
245 year represents a new generation. Means are given (±1 SE)

Year	No. focal groups	No. focal females	No. parturitions	Population density (adults/ha)	PTI (days)	Radio-tracking effort (%)
2005	8	14	17	19.0	12.1±2.44	32.9±2.05
2006	7	19	31	30.5	10.2±1.13	52.1±1.00
2007	12	29	59	6.5	7.2±0.96	67.1±0.70
2008	15	33	68	7.7	7.6±0.75	59.8±0.52
2009	9	23	43	10.4	6.5±0.73	50.9±0.65
2010	9	18	25	4.7	5.2±0.93	65.6±0.74

246 PTI is parturition trapping interval

247

248 *(i) Do ARTs arise from alternative strategies or a single strategy?* We determined whether
249 female striped mice switch tactic (consistent with a single strategy), and estimated the
250 probabilities of females moving from one tactic to another ('transition probabilities') in
251 continuous time using a general multi-state Markov model. We considered all females with
252 living relatives and >1 parturition, and assumed that individuals could move from any of the
253 three states (communal, returner, solitary) to any other state in either direction or retain a
254 single state. Transition probabilities for each state were modelled with 95% confidence
255 intervals, accounting for individual identity and parturition date. We used the msm package
256 (Jackson 2014) in R version 3.1.1. (R Development Core Team 2014).
257
258 *(ii) Do ARTs represent a mixed or a conditional strategy?* We tested for differences in
259 individual-level traits between females that subsequently use alternative tactics, as expected
260 under a conditional strategy. We used a multinomial Generalized Linear Mixed effects model
261 because this allowed us to fit female ART as a nominal response variable with three levels
262 (communal breeder, solitary breeder and returner) and BMC and AP as fixed effects. We
263 focused on females whose relatives were alive when they bred because the aim was to
264 understand tactic choice. We only considered females that were group-living when body
265 mass was recorded (conception) to determine whether differences in body mass induce
266 females to adopt different tactics, which can otherwise be confounded by the effects of
267 employing a given ART on body mass. We controlled for T_a and the interaction between
268 BMC and T_a because environmental conditions might affect females differently depending on
269 their size or body reserves. We fitted random intercepts for individual identity, natal group
270 identity and year to control for repeated measures. Considering natal group identity also
271 allowed us to control for potential effects of territory quality and genetic relatedness between
272 members of the same group, while 'year' allowed us to account for potential variation in

273 population density, predation, food availability and other unknown variables that might
274 influence tactic choice between breeding seasons. The model was executed using the package
275 MCMCglmm (Hadfield 2010; Hadfield 2012) in R; specifications and diagnostics are given
276 in Appendix S2.
277
278 To evaluate breeding synchrony, we calculated the absolute number of days between all
279 possible pairs of parturitions by different individuals up to a maximum of 23 days apart (the
280 estimate of gestation length used in our study). Where a given parturition by female A
281 occurred ±23 days from two parturitions by female B (i.e. where B gave birth ≤23 days
282 before A and again ≤23 days after A), only the record yielding the smaller date difference
283 between the pair was retained in the dataset. We noted whether each pair of females shared a
284 nest when they conceived ('nestmates'), originated in the same group but no longer shared a
285 nest when they conceived ('related non-nestmates') or originated in different groups ('non-
286 relatives'). We focused on females that were group-living when they conceived to test
287 whether breeding asynchrony is associated with females leaving the group; records
288 comparing related non-nestmates were discarded. For all records from nestmates, we
289 determined the tactics used for each pair of parturitions. This produced a categorical variable
290 ('pair category') with three levels for females that shared a nest when they conceived
291 (communal vs communal, communal vs returner, communal vs solitary), and a fourth level
292 for unrelated pairs where at least one female bred communally. Breeding synchrony data
293 were analysed in a single Generalized Linear Mixed effects Model (GLMM) with Poisson
294 errors using the lme4 package (Bates *et al.* 2014). The absolute number of days between two
295 parturitions was the response variable, year and natal group identity were random factors and
296 pair category was a fixed factor with four levels. We carried out a Dunnett multiple
297 comparison test based on this model to compare synchrony within communal breeders (i.e.

298 pairs where both individuals were communally-breeding nestmates) with synchrony between
299 communal breeders and the other three levels (returners, solitary breeders, non-relatives).
300
301 To investigate changes in the distribution of reproductive phenotypes over the breeding
302 season we fitted a Linear Mixed effects Model (LMM) to data from all four reproductive
303 phenotypes (including those that were already solitary at conception). BMC, AP, T_a and
304 reproductive phenotype were fitted as fixed effects to ordinal parturition date (i.e. where 1st
305 January of any year is day 1), controlling for female identity, group identity and year (random
306 intercepts only). This allowed us to compare parturition dates among the different
307 phenotypes.
308
309 *(iii) Is solitary breeding always the outcome of a strategy or can it also arise from entirely*
310 *extrinsic factors?* Solitary-breeding phenotypes produced by extrinsic factors (mortality of all
311 other adult female group members) occurred in the population, and so we tested whether they
312 differed in individual-level traits from females using ARTs. BMC and AP were normally-
313 distributed response variables in separate LMMs, and we fitted reproductive phenotype as a
314 fixed factor with four levels. We controlled for fixed effects of T_a and random intercepts of
315 female identity, group identity and year.
316
317 For all tests, significant effects are denoted by $P<0.05$ or a credible interval (CrI hereafter) or
318 confidence interval (CoI) that does not include zero. Continuous fixed effects were mean-
319 centred to assist model convergence. LMMs were fitted by Restricted Maximum Likelihood
320 using lme4 (Bates et al. 2014) and lmerTest (Kuznetsova, Brockhoff & Christensen 2014).
321 Tukey or Dunnett contrasts allowed us to determine which levels of factors differed from
322 each other, and *P*-values were adjusted using a single-step method (multcomp package:

323 Hothorn, Bretz & Westfal 2014). Statistical tests are two-tailed and means are least squares
324 means ± 1 SE.
325
326

327 Results

328

329 Did female striped mice switch ARTs, consistent with a single strategy?

330 Female striped mice with living relatives bred communally (40.7% of parturitions), as
331 returners (42.7%) or solitarily (17.3%). Multiple breeding attempts within a single season
332 were recorded for 55.0% of females with relatives (*n*=120 females with relatives: 1.8±0.08
333 (range 1-4) litters), of which 57.6% switched ARTs at least once (Table 2). For females that
334 bred more than once and did not switch tactic while relatives were living, the majority
335 (46.4%) bred communally, 28.6% bred as returners and 25.0% bred solitarily (Table 2).
336

337 **Table 2.** The numbers of female striped mice that showed a single reproductive phenotype (RP:
338 communal breeder, returner, solitary breeder with living relatives, solitary breeder without living
339 relatives) and those that changed from one RP to another in a single breeding season. All females
340 shown (*n*=75) produced at least two litters in a breeding season

RP	No. females
Did not switch ARTs, female relatives alive	*28*
Communal	13
Returner	8
Solitary	7
Switched ARTs, female relatives alive	*38*
communal → returner[a]	16
returner → solitary[b]	8
returner → communal[a]	6
communal → solitary	1
communal → returner → communal	3
returner → communal → returner	3
communal → returner → solitary	1
RP caused by extrinsic factor: death of female relatives	*11*
returner → solitary[b]	3
communal → solitary	1
solitary	7

341 [a]One female produced multiple litters in two consecutive seasons and is presented for the two seasons
342 separately.
343 [b]One female belongs to both these categories because she bred as a returner then twice solitarily (once before
344 and once after her relatives died).
345
346

347 Females that had living relatives and bred more than once were no more likely to switch
348 tactic than to use the same tactic throughout the breeding season (probability of switching
349 tactic: 0.58, 95% CoI=0.45 to 0.70, P=0.268, n=66; exact binomial test). A female's
350 subsequent tactic depended on her previous tactic (likelihood ratio χ^2_4 =: 44.60, P<0.001; Fig.
351 S1, Supporting information). Communal breeders were more likely to continue breeding
352 communally (β=0.013, 95% CoI=0.0190 to 0.0087) or become returners (β=0.012,
353 CoI=0.0078 to 0.0178) than to breed solitarily (β=0.001, CoI=0.0003 to 0.0041) on their next
354 breeding attempt. Returners were no more likely to continue breeding as returners (β=0.014,
355 CoI=0.0091 to 0.0209) than to switch to communal (β=0.008, CoI=0.0047 to 0.0140) or
356 solitary (β=0.006, CoI=0.0029 to 0.0108) breeding. Among those that switched tactic,
357 communal breeders were 11.5 times more likely to become returners (92 (CoI=82 to 103) %)
358 than to become solitary breeders (8 (CoI=2 to 30) %).
359
360 **Did individual-level traits influence ARTs, as expected under a conditional strategy?**
361 BMC was associated with ARTs in female striped mice with living relatives (Fig. 2; Table 3),
362 while AP, T_a and the interaction between BMC and T_a were not (Table 3). Solitary breeders
363 with relatives were heavier at conception than females that bred communally and returners,
364 but there was no difference in BMC between communal breeders and returners (Fig. 2).
365 Among females that had living relatives and went on to breed solitarily, body mass did not
366 differ between females that were group-living at conception (51.3±1.87, n=18 observations
367 from 18 females that became solitary after conception), and those that were already solitary
368 when they conceived (47.8±1.90, n=19 observations from 16 females; β=3.52±2.04, t=1.72,
369 P=0.099, controlling for AP and T_a).
370

371 **Table 3.** Multinomial Mixed effects Model to test for the effects of body mass at conception (BMC),
372 age at parturition (AP), minimum ambient temperature (T_a) and the interaction between T_a and BMC
373 on ARTs in female striped mice with living relatives (*n*=195 records from 112 individuals that were
374 group-living when they conceived). We fitted unique variance and co-variance structures for each
375 ART ('communal breeder', 'solitary breeder', 'returner') interacted with each random term
376 (individual identity, group identity and year; not shown). Parameter estimates (β) are modes from the
377 posterior distribution with 95% credible intervals. Non-significant fixed effects were eliminated
378 sequentially to reach the final model. Significant effects are in bold.

Fixed effects	***β***	***p*MCMC**
communal breeder intercept	2.524 (0.603 to 4.586)	**0.007**
returner intercept	2.738 (1.147 to 4.535)	**0.001**
BMC[a] (communal)	-0.157 (-0.274 to -0.047)	**0.003**
BMC[a] (returner)	-0.121 (-0.230 to -0.016)	**0.021**
T_a[a] (communal)	0.066 (-0.174 to 0.314)	0.605
T_a[a] (returner)	0.132 (-0.099 to 0.369)	0.246
AP[a] (communal)	0.005 (-0.004 to 0.015)	0.290
AP[a] (returner)	0.005 (-0.004 to 0.014)	0.296
T_a × BMC[a] (communal)	-0.024 (-0.052 to 0.003)	0.078
T_a × BMC[a] (returner)	-0.023 (-0.049 to 0.003)	0.080

379 [a] 'solitary breeder' is the baseline level of the response (reference group)

380

381

382 The returner tactic was more likely to occur because returners moved to a new nest (n=69
383 parturitions from 53 individuals) than because they stayed behind when their nestmates
384 moved away (n=18 parturitions from 18 individuals; probability of returner tactic arising
385 through movement of focal female versus relatives: 0.75, 95% CoI=0.63 to 0.84, P<0.001,
386 exact binomial test). There was no difference between returners that moved and those that
387 stayed behind in AP (β=-0.005±0.003, Z=1.60, P=0.110), BMC (β=-0.02±0.04, Z=0.54,
388 P=0.589) or the number of females they shared a nest with before parturition (β=0.25±0.17,
389 Z=1.48, P=0.138; GLMM with binomial errors controlling for individual and group identities
390 and year). Groups were more likely to reunite because the returner moved back (n=58
391 parturitions from 46 individuals) than because the returners' relatives moved to join her at her
392 new nest (n=29 parturitions by 27 individuals; probability of re-joining group owing to
393 movement of returner versus relatives: 0.67 (0.56 to 0.76), P=0.002).
394
395 Returners gave birth 1.7±0.35 (range 0-28) days after becoming temporarily solitary (n=84
396 parturitions by 63 females), and re-joined the group after 6.4±0.61 (range 1-35) days alone.
397 On average, they re-joined the group after their communally-breeding nestmates had given
398 birth (mean difference=7.7±1.95 days; t_{89}=3.82, P<0.001, paired t-test). The interval between
399 leaving the group and parturition was not influenced by BMC (β=0.00002±0.01, Z=0.001,
400 P=0.999, GLMM with poisson errors controlling for individual and group identities and year)
401 or AP (β=-0.0006±0.001, Z=0.53, P=0.600). Those that moved to a new nest stayed away for
402 longer than those that stayed behind when their relatives moved away (changed nest:
403 6.8±0.72 nights; stayed: 4.0±0.65 nights; β=0.40±0.18, Z=2.27, P=0.023; GLMM with
404 poisson errors). The number of nights that returners spent away was not related to BMC
405 (β=0.01±0.01, Z=1.41, P=0.158) or AP (β=-0.0002±0.001, Z=0.22, P=0.823).
406

Females with living relatives were more likely to become solitary by moving to a new nest (n=18 individuals) than by remaining at the nest when their nestmates moved away (n=7; probability of becoming solitary by moving away: 0.72, 95% CoI=0.51 to 0.88, P=0.043). All seven females in the latter category had only one female relative, while those that moved to a new nest came from larger groups (1.9±0.31 female nestmates, range 1-5; Z=2.05, P=0.040, asymptotic Wilcoxon Rank Sum Test). There was no difference between solitary females that moved to a new nest and those whose nestmates moved in age (β=0.001±0.003, Z=0.25, P=0.806) or BMC (β=0.009±0.056, Z=0.16, P=0.876, GLMM with binomial errors controlling for year and group identity) with regard to their first solitary breeding attempt. Solitary breeders left the group before their communally-breeding nestmates gave birth (mean difference=-19.35±4.45 days; t_{20}=6.39, P<0.001, paired t-test).

The interval between leaving the group and giving birth was longer for solitary breeders with relatives (12.9±3.7 days, n=25) than for returners (β=1.28±0.18, Z=6.99, P<0.001, GLMM with poisson errors controlling for individual and group identities and year). Among solitary breeders (n=25), 56% gave birth within six (median 0) days of leaving the nest, while 28% did not appear to be gestating when they left the nest (26-37 day interval between leaving the nest and parturition). The interval between becoming solitary and giving birth increased with AP (β=0.002±0.001, Z=2.2, P=0.025; n=25, GLMM with poisson errors controlling for group identities and year) and the number of female nestmates (β=0.146±0.002, Z=66.3, P<0.001) and decreased with increasing BMC (β=-0.065±0.02, Z=29.7, P<0.001).

Was breeding synchrony associated with ARTs?

Communally-breeding females from the same group were more synchronized with each other in giving birth (5.8±0.49 days apart, n=61 pairs of observations from 44 individuals) than

females from different groups were with each other (9.0±0.57 days apart, n=1938 pairs from 132 individuals; β=0.43±0.06, Z=7.68, P<0.001). Communally-breeding nestmates were also more synchronized with each other than with returners from their own group (7.1±0.56 days apart, n=63 pairs from 54 individuals; β=0.19±0.07, Z=2.70, P=0.018), but synchrony within communal breeders did not differ from synchrony between communal and solitary breeders from the same group (5.1±0.70 days apart, n=12 pairs from 16 individuals; β=0.13±0.13, Z=1.06, P=0.622). Returners were no more likely to give birth before communally-breeding nestmates (n=31 pairs from 33 individuals) than after them (n=31 pairs from 37 individuals; P=1.000, exact binomial test; 1 pair of observations in which a communal breeder and a returner gave birth on the same day excluded), nor were solitary breeders more likely to give birth before communally-breeding nestmates (n=5 pairs from 8 individuals) than after them (n=7 pairs from 10 individuals; P=0.774).

Did the distribution of reproductive phenotypes change over the breeding season?

Communal breeders gave birth earlier in the season than females of any other category (Tukey contrasts based on LMM: $P \leq 0.004$; Fig. 3); solitary females with and without relatives and returners did not differ in the timing of their parturitions ($P \geq 0.297$; Fig. 3), controlling for T_a (β=2.44±0.34, t=7.28, P<0.001) and BMC (β=0.66±0.18, t=3.60, P<0.001), which were positively related to parturition date. Age did not influence parturition date (β=-0.01±0.01, t=0.95, P=0.342).

Solitary breeding as a consequence of extrinsic factors

Of the 45 females that bred solitarily, 57.8% had surviving female relatives in the population. The rest were constrained to breed solitarily because their female relatives died, and they did not join another group with unrelated females. Females that became solitary because their relatives died did not differ in BMC from communal breeders (β=2.48±1.59, Z=1.56, P=0.242; LLM with Dunnett contrasts; Fig. 2) or returners (β=1.28±1.52, Z=0.84, P=0.680). However, females that were group-living at conception and became solitary while their relatives were living weighed more than females whose relatives died (β=4.81±2.01, Z=2.39, P=0.040; Fig. 2). BMC did not differ before and after females' relatives died (before relatives died: 48.22±3.50g, n=4 records from 4 females, after: 48.50±1.37g, n=17 observations from 25 females; β=-0.28±3.71, t=0.07, P=0.941), controlling for AP (β=0.03±0.01, t=2.25, P=0.033). Solitary females without relatives did not differ in AP (299.5±21.87 days) from communal breeders (297.2±16.24 days; β=2.32±21.79, Z=0.11, P=0.999; LMM with Dunnett contrasts) or returners (298.4±15.86 days; β=1.14±20.93, Z=0.06, P=0.999). There was a tendency for solitary females with living relatives to be younger (245.4±20.71 days) than those whose relatives had died (β=54.15±24.06, Z=2.25, P=0.056).

Discussion

We tested whether the theoretical framework developed to explain strategies governing male ARTs also applies to females. Among female striped mice, three ARTs occurred simultaneously in the population: most females bred communally in a nest shared with relatives (communal breeders) or left the group temporarily to give birth (returners). A smaller proportion became solitary and did not return to the group after producing young,

478 even though relatives were still living (solitary breeders with relatives). Females switched
479 between ARTs, which can occur under single but not alternative strategies, and so we tested
480 whether this represented a conditional or mixed single strategy. Studies of conditional
481 strategies in free-living individuals are often unable to measure potential cues (e.g. body
482 mass) before individuals switch tactic, and are thus often confounded by environmental
483 effects that occur after the switch. We addressed this by investigating body mass records
484 collected before females became solitary. Females that went on to breed solitarily were
485 heavier than communal breeders and returners, which suggests that body mass influences
486 tactic choice. We could differentiate between two kinds of solitary breeder: those that became
487 solitary while their relatives were alive and those that were forced by stochastic external
488 factors (mortality of relatives) to rear young alone. We did not find an association between
489 female reproductive phenotype and either parturition trapping interval and radio-tracking
490 effort, which suggests that variation in survey effort did not bias our results towards a
491 particular phenotype. Our results show that both phenotypic plasticity and extrinsic factors
492 can produce intra-specific variation in social organization, and that evolutionary theory
493 developed for ARTs in males also applies in females.
494
495 *(i) Do ARTs arise from alternative strategies or a single strategy in female striped mice?*
496 The majority of female striped mice that bred more than once switched reproductive tactics.
497 The ability to switch ARTs has been described in females of several species of birds, fish and
498 insects (Warner 1985; Åhlund & Andersson 2001; Zink 2003). This behaviour is consistent
499 with a single strategy, where different tactics arise from one decision-rule (Schradin &
500 Lindholm 2011). It is worth noting, however, that several females that bred more than once
501 did not switch tactics. Instead they showed a single phenotype of solitary breeder, communal
502 breeder or returner. Those females could be following i) alternative strategies with fixed

503 tactics or ii) a single strategy in the absence of (or without responding to) cues that elicit
504 switching between tactics. Strategic models show that alternative and plastic strategies can
505 coexist within a single population and be evolutionarily stable under a range of conditions
506 (Lively 1986; Plaistow et al. 2004). This idea has received further theoretical support from a
507 quantitative genetics perspective (Hazel, Smock & Lively 2004). Indeed, empirical work has
508 described coexistence of conditional and unconditional strategies in barnacles (Lively et al.
509 2000), mites (Buzatto, Simmons & Tomkins 2012) and sailfin mollies (Fraser et al. 2014). In
510 our study, many females that switched tactics had previously maintained one tactic for
511 multiple breeding attempts before the switch. It therefore seems likely that at least some of
512 the females that did not switch tactic were capable of doing so. In striped mice, high
513 population density can constrain females to remain group-living (the best tactic under these
514 conditions; Schradin et al 2010), while experimentally easing these constraints by decreasing
515 local population density induces a switch to solitary-living (Schoepf & Schradin 2012a). The
516 decision not to switch tactics can therefore represent an adaptive response to stable
517 environmental conditions. While we cannot exclude the possibility that females that
518 maintained the same tactic throughout the breeding season were using alternative strategies,
519 we present evidence for the existence of a plastic strategy that is used by most females in the
520 population.
521
522 A female's reproductive tactic was a predictor of her subsequent tactic, with individuals often
523 following the same tactic for more than one consecutive breeding attempt. Females that
524 switched tactics generally proceeded from communal breeder to returner to solitary. The
525 relative distribution of ARTs changed over the breeding season, with communal breeding
526 occurring earlier in the season than the other ARTs. Tactic switches between communal
527 breeders and returners were often reversible. Solitary breeders, by definition, do not re-join

528 their former group, but can make the transition to communal breeder (or returner) by forming
529 plural breeding groups with adult daughters. One female established a new group after her
530 relatives died, and she and her daughters bred communally the following year. Females
531 whose nestmates died did not join other groups, indicating the importance of genetic kinship
532 in the formation of breeding groups. Although non-relatives can form transient overnight
533 huddling groups in winter (Schradin, Schubert & Pillay 2006), aggression towards non-kin
534 during the breeding season (Schradin 2004) probably constrains the direction of tactic
535 switching.
536
537 *(ii) Do ARTs represent a mixed or a conditional strategy?*
538 Mixed and conditional strategies are two types of single strategy (Schradin & Lindholm
539 2011). When individuals follow a conditional strategy, ARTs can be determined by
540 differences in traits that reflect competitive ability (Gross 1996). No such association is
541 predicted under a mixed strategy, which assumes that tactics are stochastically assigned
542 (Dominey 1984). We found that solitary breeders with relatives were heavier than communal
543 breeders and returners before leaving the group, consistent with a conditional strategy (Fig.
544 4). Body mass or size is an important cue governing the switchpoint between ARTs in males
545 (e.g. Tomkins & Brown 2004; Schradin et al. 2009b) and females (Warner 1985) of various
546 taxa. This probably reflects its reliability as an indicator of competitive ability (Wada et al.
547 2005) and/or energy reserves (Nunes et al. 1999) in species with alternative life histories.
548 Male and female Belding's ground squirrel (*Spermophilus beldingi*), for example, do not
549 disperse until they reach a threshold body mass, and dispersing males have more fat reserves
550 than males of the same age that delay dispersal (Nunes et al. 1999). Thermoregulation is
551 more energetically expensive in solitary than group-living striped mice (Scantlebury et al.
552 2006), and solitary breeders must also meet the energetic requirements of nursing pups and

553 defending a territory alone. We therefore propose that female striped mice remain group-
554 living until they have amassed enough body reserves to support the energetic demands of
555 solitary breeding. Together these results show that body mass is a key trait underlying the
556 evolution of conditional strategies in many species.
557
558 Leaving the group temporarily to give birth may allow females to avoid reproductive
559 competition without foregoing the long-term benefits of group-living. Female lions (*Panthera*
560 *leo*) become less gregarious during the first weeks postpartum and hide cubs from pridemates
561 (Packer, Pusey & Eberly 2001). Breeding synchrony is thought to have evolved to reduce the
562 risk of infanticide by co-breeding females (Lambin 1993; Poikonen *et al.* 2008), which stop
563 being infanticidal after their own offspring are born (e.g. McCarthy & Saal 1985). In
564 addition, asynchronous births are associated with higher pup mortality for later-born litters in
565 some cooperatively breeding mammals because younger pups are outcompeted by older ones
566 or suffer physical trauma from being crushed by them (Mennella *et al.* 1990; Hodge, Bell &
567 Cant 2011). Indeed, we found that the degree of within-group breeding synchrony was lower
568 for returners than communal breeders. This suggests that the returner tactic might have
569 evolved as a counter-measure against infanticide and/or offspring competition with older
570 litters. Interestingly, females that left the group without returning did not differ in synchrony
571 from communal breeders, which suggests that synchrony did not underlie their decision to
572 breed solitarily.
573
574 *(iii) Solitary breeding as a consequence of extrinsic factors*
575 Group-living females can become solitary of their own volition or because of external
576 constraints. Among the females that bred solitarily in our study, 57.8% had surviving female
577 relatives in the population and the rest became solitary because their relatives had died.

578 Importantly, the latter group weighed less than solitary breeders with living relatives, but did
579 not differ from group-living females in body mass. This suggests that solitary breeders
580 without relatives would have usually remained group-living if their relatives had survived.
581 The trend towards females with no relatives being older than solitary females with relatives
582 may be a consequence of the former having outlived their relatives. In summary, extrinsic
583 factors can produce a solitary-breeding phenotype that differs in individual-level traits from
584 females that become solitary through choice.
585
586 *Potential fitness outcomes*
587 Alternative phenotypes can persist within a population when relative fitness rankings reverse
588 across different spatial or temporal units (Moran 1992). Relative fitness varies between years
589 in male striped mice: in years with high population density dominant breeding males sired
590 more pups than roamers and philopatric males, whereas all males were roamers in years with
591 low population density (Schradin & Lindholm 2011). It is not yet known whether fitness
592 differs between ARTs in female striped mice, and whether relative fitness rankings vary
593 under different ecological conditions (e.g. population density). In our study, communal
594 breeders gave birth ~11 days earlier than returners and ~16 days before solitary breeders. The
595 abundance of food plants at our study site decreased linearly over the breeding season (D.L.
596 Hill, Pillay, N. & Schradin, C., unpublished data). This raises the possibility that communal
597 breeders' offspring could experience greater food availability. This may be traded-off with
598 the greater risk of infanticide in communally-breeding groups (Schradin et al. 2010).
599 Comparisons of fitness correlates between solitary and communally-breeding female rodents
600 have yielded mixed results (e.g. Boyce & Boyce 1988, Manning et al. 1995). Whether free-
601 living offspring born in communal and solitary nests differ in growth trajectories, condition
602 or survival remains to be tested in female striped mice.

603

604 *Conclusions and implications*

605 Male ARTs usually evolve where investment by dominant resource-holding ('bourgeois')
606 males can be exploited by other males (Taborsky, Oliveira & Brockmann 2008). However,
607 owing to anisogamy, and gestation in viviparous species, all breeding females must make a
608 substantial investment in reproduction, resulting in smaller asymmetries in effort and fitness
609 between females compared to males (Taborsky, Oliveira & Brockmann 2008). Consequently,
610 ARTs are usually more subtle in females than in males and more likely to occur after
611 fertilisation. Female striped mice show three ARTs whose expression is controlled by a single
612 strategy (Fig. 4) in at least the majority of the population. This strategy may enable females to
613 avoid reproductive competition when certain individual-level and environmental conditions
614 are met. Male and female ARTs share many similarities in striped mice, but also differ in
615 certain respects. Males, like females, follow three ARTs that differ in body mass; they can
616 breed solitarily (as roamers) or in a group (as dominant breeders or philopatrics; Schradin et
617 al. 2009b). Philopatric males differ in age from dominant breeders and roamers (Schradin et
618 al. 2009b), but age did not influence female ARTs in our study. At a proximate level, males
619 following alternative tactics differ in corticosterone and testosterone levels (Schradin et al.
620 2009b), whereas female ARTs differ in corticosterone and oestrogen levels but not in
621 testosterone (Hill, Pillay & Schradin 2015). These differences and the occurrence of the
622 returner tactic in females suggest that ARTs in female striped mice are unlikely to simply
623 reflect a correlated response to selection for ARTs in males.

624

625 An important feature of populations in which reproductive and social tactics occur in both
626 sexes is the potential for the entire social system to change facultatively as a result of
627 decisions made at the individual level (Schradin et al 2012). Social flexibility has been

628 described in various taxa, including dunnocks (*Prunella modularis*), burying beetles
629 (*Nicrophorus vespilloides*) and humans (*Homo sapiens*, reviewed in Schradin et al. 2012). It
630 is particularly prevalent in species where individuals need to respond quickly to
631 unpredictable, fluctuating environmental conditions that might differ substantially from those
632 experienced by previous and subsequent generations (Schradin et al. 2012). Improving our
633 understanding of the evolution of phenotypic plasticity and how it facilitates resilience to
634 environmental change is an important and timely goal.

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636

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647

Data accessibility

Data to be made available from the Dryad Digital Repository (Hill, Pillay & Schradin unpublished).

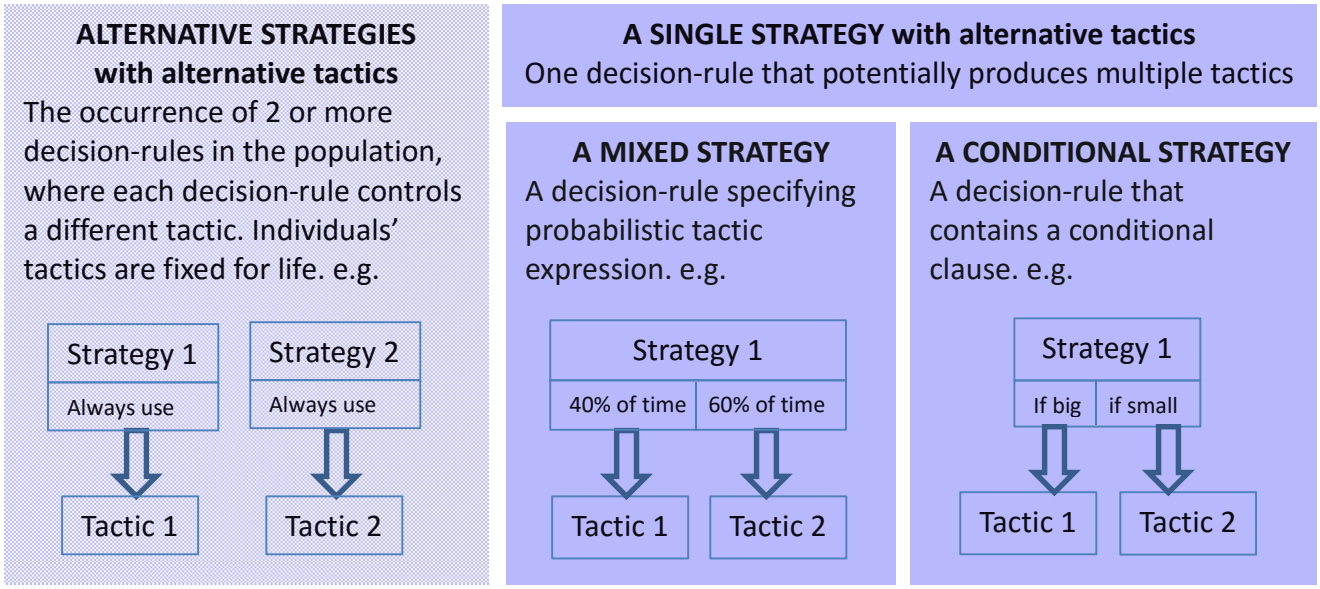
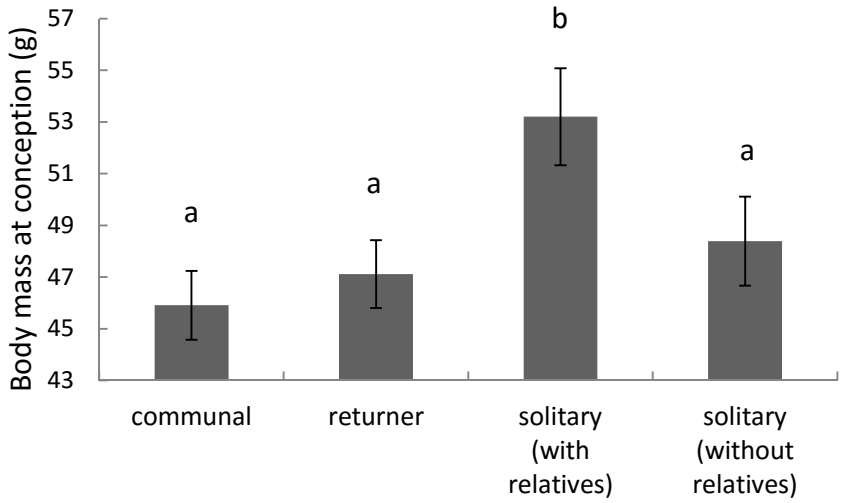


Fig. 1. Genetically-based decision-rules called strategies govern alternative reproductive tactics in members of the same sex and population. In species with *alternative strategies*, each strategy controls a different tactic with canalized expression (i.e. phenotypes are robust to environmental or genetic perturbations). In species with a *single strategy*, individuals use one decision-rule that controls the expression of multiple phenotypes (Schradin et al. 2012). Single strategies can be divided into mixed or conditional strategies. Mixed strategies specify that individuals switch tactics according to a particular probability distribution or are assigned permanently-adopted tactics probabilistically (Dominey 1984). Conditional strategies occur when each individual selects the tactic that generates the highest fitness returns for its prevailing circumstances (Gross 1996). The scenarios represented above are not necessarily mutually exclusive within a population (e.g. Plaistow et al. 2004)

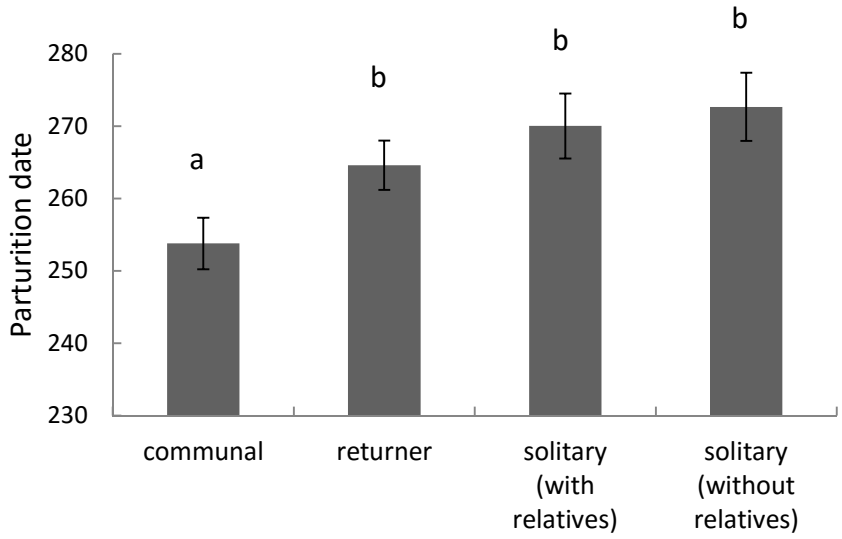
676



677

678 **Fig. 2.** Mean body mass at conception ±1SE in communal breeders (*n*=87 parturitions by 64
679 individuals), returners (*n*=90 parturitions from 66 females) and solitary breeders with living relatives
680 (*n*=18 parturitions by 18 females that were still group-living when body mass was measured) and
681 without living relatives (*n*=29 parturitions by 20 females). Different letters above bars represent
682 significant differences adjusted for False Discovery Rate. Note that the y-axis is truncated

683



684
685 **Fig. 3.** Mean parturition date ±1SE (1 Jan of any year=day 1) in communal breeders (*n*=87
686 parturitions by 64 individuals), returners (*n*=90 parturitions by 66 individuals) and solitary breeders
687 with living relatives (*n*=37 parturitions by 26 individuals) and without relatives (*n*=29 parturitions by
688 20 individuals). Different letters above bars represent significant differences adjusted for multiple
689 testing
690

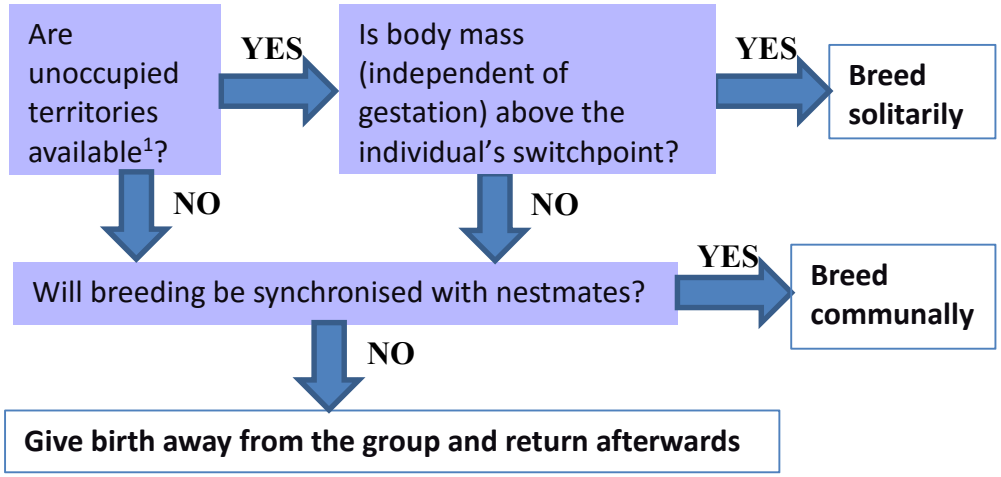


Fig. 4. The strategy (evolved set of decision-rules) predicted to govern the expression of the three alternative reproductive tactics used by female striped mice with living relatives. This ties together results from the present study and [1]Schradin, König & Pillay (2010). Females switched tactic upon reaching thresholds of body mass or breeding asynchrony with nestmates. Those that became solitary breeders were heavier when they conceived than communal breeders and returners, which did not differ in body mass. Females that were less closely synchronized with nestmates were more likely to use a returner tactic than to give birth communally. Selection is thought to act upon heritable genetic variation for the position of the switchpoint, so different individuals might change tactics at different values of the underlying traits (Tomkins & Hazel 2007). Solitary-breeding phenotypes can arise either from this strategy or as a consequence of extrinsic stochastic processes (mortality of all adult female relatives)

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Supporting Information

The following Supporting Information is available for this article online:

Appendix S1. Methods for multiple imputation of missing body mass and age values

Appendix S2. Specifications for multinomial mixed effects model

Figure S1. Correspondence between 97 consecutive pairs of alternative reproductive tactics (ARTs) represented by $\chi 2$ distances between points in female striped mice